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Morton, J. 1987. Sour Orange. p. 130–133. In: Fruits of warm climates. Julia F. Morton, Miami, FL.

Sour Orange

S8 #14

Citrus aurantium

A species of multiple uses, the sour orange *(Citrus aurantium,* L.), is also known as bitter, bigarade, or Seville orange. In Spanish-speaking areas it may be called *naranja ácida, naranja agria,* or *naranja amarga.* In Arabia, it is *naranji;* in Italy, *melangolo;* in India, *khatta;* in Samoa, *moli,* in Guam, soap orange.

Description

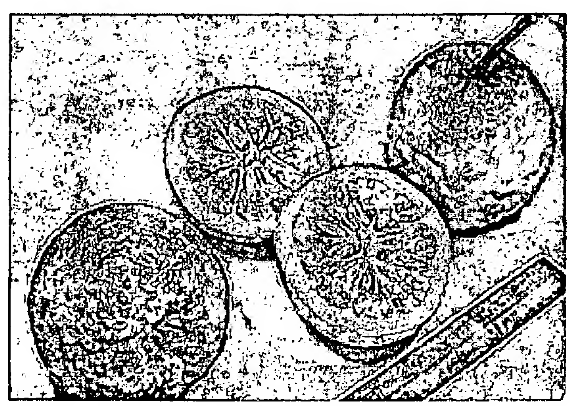

Fig. 35: The sour orange *(Citrus aurantium)*has a rough, fairly thick skin, very sour juice.

The tree ranges in height from less than 10 ft (3 m) to 30 ft (9 m), is more erect and has a more compact crown than the sweet orange; has smooth, brown bark, green twigs, angular when young, and flexible, not very sharp, thorns from 1 in to 3 1/8 in (2.5-8 cm) long. The evergreen leaves (technically single leaflets of compound leaves), are aromatic, alternate, on broad-winged petioles much longer than those of the sweet orange; usually ovate with a short point at the apex; 2 1/2 to 5 1/2 in (6.5-13.75 cm) long, 1 1/2 to 4 in (3.75-10 cm) wide; minutely toothed; dark-green above, pale beneath, and dotted with tiny oil glands. The highly fragrant flowers, borne singly or in small clusters in the leaf axils, are about 1 1/2 in (3.75 cm) wide, with 5 white, slender, straplike, recurved, widely-separated petals surrounding a tuft of up to 24 yellow stamens. From 5 to 12% of the flowers are male.

The fruit is round, oblate or oblong-oval, 2 3/4 to 3 1/8 in (7-8 cm) wide, rough-surfaced, with a fairly

thick, aromatic, bitter peel becoming bright reddish-orange on maturity and having minute, sunken oil glands. There are 10 to 12 segments with bitter walls containing strongly acid pulp and from a few to numerous seeds. The center becomes hollow when the fruit is full-grown.

Origin and Distribution

The sour orange is native to southeastern Asia. Natives of the South Sea Islands, especially Fiji, Samoa, and Guam, believe the tree to have been brought to their shores in prehistoric times. Arabs are thought to have carried it to Arabia in the 9th Century. It was reported to be growing in Sicily in 1002 A.D., and it was cultivated around Seville, Spain, at the end of the 12th Century. For 500 years, it was the only orange in Europe and it was the first orange to reach the New World. It was naturalized in Mexico by 1568 and in Brazil by 1587, and not long after it was running wild in the Cape Verde Islands, Bermuda, Jamaica, Puerto Rico and Barbados. Sir Walter Raleigh took sour orange seeds to England; they were planted in Surrey and the trees began bearing regular crops in 1595, but were killed by cold in 1739.

Spaniards introduced the sour orange into St. Augustine, Florida. It was quickly adopted by the early settlers and local Indians and, by 1763, sour oranges were being exported from St. Augustine to England. Sour orange trees can still be found in Everglades hammocks on the sites of former Indian dwellings. The first sweet orange budwood was grafted onto sour orange trees in pioneer dooryards and, from that time on, the sour orange became more widely grown as a rootstock in all citrus-producing areas of the world than for its fruit or other features. Today, the sour orange is found growing wild even in southern Georgia and from Mexico to Argentina.

It is grown in orchards or groves only in the Orient and the various other parts of the world where its special products are of commercial importance, including southern Europe and offshore islands, North Africa, the Middle East, Madras, India, West Tropical Africa, Haiti, the Dominican Republic, Brazil and Paraguay.

Varieties

There are various well-established forms of the sour orange. In the period 1818-1822, 23 varieties were described and illustrated in Europe. A prominent subspecies is the Bergamot orange, C. *aurantium,* var. *bergamia* Wight & Arn., grown in the Mediterranean area since the 16th Century but commercially only in Italy. Trees grown in California and Florida under this name are actually the 'Bouquet' variety of sour orange (see below). The flowers of the Bergamot are small, sweetly fragrant; the fruits round or pear-shaped, with strongly aromatic peel and acid pulp.

The myrtle-leaved orange (C. *aurantium,* var. *myrtifolia),* is a compact shrub or tree with small leaves and no thorns. It was found as a bud mutation on trunks of old sour orange trees in Florida. It is propagated and grown only on the French and Italian Riviera for its small fruits which are preserved in brine and exported for candying.

Apart from these special types, there are several groups of sour oranges, within which there are placed certain cultivars:

1) *Normal group* (large, seedy fruits)

'African', 'Brazilian', 'Rubidoux', 'Standard', 'Oklawaha' and 'Trabut'. 'Oklawaha' originated in the United States. It has large fruits rich in pectin and is prized for marmalade.

2) Aberrant group

'Daidai', or 'Taitai', popular in Japan and China. Its fruits are large with very thick peel, very acid pulp, and many seeds. The tree is somewhat dwarf and almost thornless; immune to citrus canker in the Philippines. It is prized for its flower buds which are dried and mixed with tea for their scent.

'Goleta' has medium-large fruits with juicy, medium-sour pulp and very few seeds. The tree is of medium size and almost thornless.

'Bouquet' has small, deep-orange fruits, acid, with few seeds. The tree is less than 10 ft (3 in) high and is grown as an ornamental.

3) *Bittersweet group* includes any sweet-acid forms of the sour orange introduced by Spaniards and formerly found growing in the Indian River region of Florida. These oranges are often seen in a naturalized state in the West Indies. The peel is orange-red, the pulp is darker in hue than that of the normal sour orange.

'Paraguay' was introduced from Paraguay in 1911. The fruit is of medium size, with sweet pulp, moderately seedy. The tree is large, thorny and hardy.

Among other forms of sour orange, there is in India a type called 'Karna', 'Khatta' or 'Id Nimbu', identified as *C. aurantium* var. *khatta* (or *C. karna* Raf.) but suspected of being a hybrid of sour orange and lemon. The fruits are typical sour oranges but the flowers are red-tinted like those of the lemon.

Two cultivars are grown as rootstocks for the sweet orange in China:

'Vermilion Globe' has oblate fruits containing 30 to 40 seeds. The tree has long, narrow, pointed

'Leather-head' has small, oblate, rough fruits with 20 seeds. The tree has elliptic, blunt leaves.

Cultivars grown especially for the production of Neroli oil in France and elsewhere, have flowers in large, more concentrated clusters than the ordinary types of sour orange. One of these, 'Riche Défouille', has unusual, wingless leaves.

Climate

The sour orange flourishes in subtropical, near-tropical climates, yet it can stand several degrees of frost for short periods. Generally it has considerable tolerance of adverse conditions. But the Bergamot orange is very sensitive to wind and extremes of drought or moisture.

Soil

Unlike its sweet relative, the sour orange does well on low, rich soils with a high water table and is adapted to a wide range of soil conditions.

Propagation

Sour orange trees volunteer readily from self-sown seeds. As generally grown for rootstock for sweet oranges, they are raised in nurseries for 1 or 2 years and then budded. Growth of the seedlings, especially in diameter, has been expedited by weekly applications of gibberellic acid to the stems,

making it possible to bud them much earlier.

Culture

In the proper climatic and soil conditions, the sour orange is self-maintaining and receives only a modicum of cultural attention. It has an extraordinary ability to survive with no care at all. Some trees in Spain are said to be over 600 years old and one tree in a tub at Versailles, which, of course, must be carefully tended, was reportedly planted in the year 1421.

Pests and Diseases

The sour orange is subject to most of the pests that attack the sweet orange. In addition to its susceptibility to the disease called tristeza, the tree is liable to other viruses -crinkly leaf, gummy bark, psorosis, and xyloporosis. The Division of Plant Industry of the Florida State Department of Agriculture has recorded the following fungal problems as sometimes seen: leaf spot *(Alternaria citri, Cercospora penzigii, Mycophaerella horii, Cladosporium oxysporum,* and *Phyllosticta hesperidearum);* greasy spot *(Cercospora citri-grisea);* tar spot (C. *gigantea);* leprosis *(Cladosporium herbarum);* mushroom root rot *(Clitocybe tabescens);* anthracnose *(Colletotrichum gloeosporioides);* thread blight *(Corticium koleroga* and C. *stevensii);* gummosis and dieback *(Diaporthe citri);* foot rot and root rot *(Fusarium oxysporum, Macrophomia phaseolina, Phytophthora* spp.); heart rot and wood rot *(Fomes applanatus, Ganoderma sessilis, Xylaria polymorpha),* and others.

Food Uses

The normal types of sour orange are usually too sour to be enjoyed out-of-hand. In Mexico, however, sour oranges are cut in half, salted, coated with a paste of hot chili peppers, and eaten.

The greatest use of sour oranges as food is in the form of marmalade and for this purpose they have no equal. The fruits are largely exported to England and Scotland for making marmalade. Sour oranges are used primarily for marmalade in South Africa.

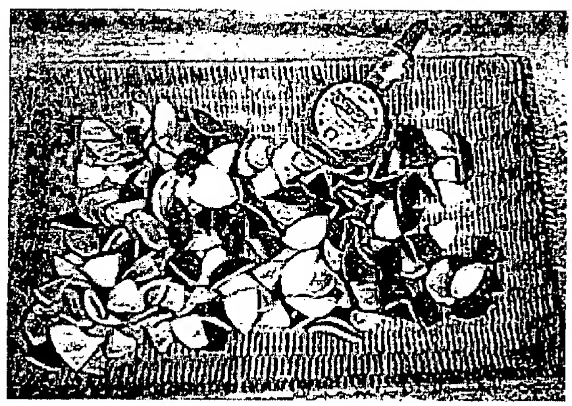

Fig. 36: Dried peel of the locally-grown sour orange yields the essential oil that flavors "Curacao liqueur".

The juice is valued for ade and as a flavoring on fish and, in Spain, on meat during cooking. In Yucatan, it is employed like vinegar. In Egypt and elsewhere, it has been fermented to make wine.

"Bitter orange oil", expressed from the peel, is in demand for flavoring candy, ice cream, baked goods, gelatins and puddings, chewing gum, soft drinks, liqueurs and pharmaceutical products, especially if the water-or alcohol-insoluble terpenes and sesquiterpenes are removed. The oil is produced in Sicily, Spain, West Africa, the West Indies, Brazil, Mexico and Taiwan.

The essential oil derived from the dried peel of immature fruit, particularly from the selected types - 'Jacmel' in Jamaica and the much more aromatic 'Curacao orange' (var. *curassaviensis)-gives* a distinctive flavor to certain liqueurs.

"Neroli oil", or "Neroli Bigarade Oil", distilled from the flowers of the sour orange, has limited use in flavoring candy, soft-drinks and liqueurs, ice cream, baked goods and chewing gum.

'Petitgrain oil', without terpenes, is used to enhance the fruit flavors (peach, apricot, gooseberry, black currant, etc.) in food products, candy, ginger ale, and various condiments.

'Orange leaf absolute' enters into soft-drinks, ice cream, baked goods and candy.

The ripe peel of the sour orange contains 2.4 to 2.8%, and the green peel up to 14%, neohesperidin dihydrochalcone which is 20 times sweeter than saccharin and 200 times sweeter than cyclamate. Potential use as a sweetener may be hampered by the limited supply of peel.

Food Value Per 100 g of Edible Portion

	Fruit (raw)	*Fruit (raw, with only superficial layer of peel removed)**
Calories	37-66	
Moisture	83-89.2 g	77.8-83.1 g
Protein	0.6-1.0 g	0.154-0.167 g
Fat	trace-0.1 g	0.05-0.07 g
Carbohydrates	9.7-15.2 g	?
Fiber	0.4 g	1.8-2.2 g
Ash	0.5 g	0.57-0.69 g
Calcium	18-50 mg	64.3-81.9 mg
Iron	0.2 mg	0.22-0.85 mg
Phosphorus	12 mg	19.6-20.4 mg
Vitamin A	290 mcg or 200 I.U.	0.055-0.07 mg
Thiamine	100 mcg	0.048-0.059 mg
Riboflavin	40 mcg	0.030-0.040 mg
Niacin	0.3 mg	0.282-0.400 mg
Ascorbic Acid	45-90 mg	55.2-103.5 mg
*Sampled in Guatemala and El Salvador.		

Other Uses

Soap substitute: Throughout the Pacific Island, the crushed fruit and the macerated leaves, both of which make lather in water, are used as soap for washing clothes and shampooing the hair. Safford described the common scene in Guam of women standing in a river with wooden trays on which they rub clothing with sour orange pulp, then scrub it with a corncob. He wrote: "Often the entire surface of the river where the current is sluggish is covered with decaying oranges." On the islands of Zanzibar and Pemba, the fruits are used for scouring floors and brass.

Perfumery: All parts of the sour orange are more aromatic than those of the sweet orange. The flowers are indispensable to the perfume industry and are famous not only for the distilled Neroli oil but also for "orange flower absolute" obtained by fat or solvent extraction. During favorable weather in southern

France, 2,200 lbs (1,000 kg) of flowers will yield 36 to 53 oz (1,000-1,500 g) of oil.

Neroli oil consists of 35% terpenes (mainly dipentene, pinene and camphene), 30% *l*-linalool, and 4% geraniol and nerol, 2% *d*-terpineol, 6% *d*-nerolidol, traces of decyclic aldehyde, 7% *l*-linalyl acetate, 4% neryl and geranyl acetates, traces of esters of phenylacetic acid and benzoic acid, as much as 0.1% methyl anthranilate, and traces of jasmone, farnesol, and palmitic acid. Orange flower water is usually a by-product of oil production.

Petitgrain oil is distilled from the leaves, twigs and immature fruits, especially from the Bergamot orange. Both Petitgrain and the oil of the ripe peel are of great importance in formulating scents for perfumes and cosmetics. Petitgrain oil is indispensable in fancy eau-de-cologne. The seed oil is employed in soaps.

Honey: The flowers yield nectar for honeybees.

Wood: The wood is handsome, whitish to pale-yellow, very hard, fine-grained, much like boxwood. It valued for cabinetwork and turnery. In Cuba it is fashioned into baseball bats.

Medicinal Uses: Sour orange juice is antiseptic, anti-bilious and hemostatic. Africans apply the cut-open orange on ulcers and yaws and areas of the body afflicted with rheumatism. In Italy, Mexico and Latin America generally, decoctions of the leaves are given for their sudorific, antispasmodic, stimulant, tonic and stomachic action. The flowers, prepared as a sirup, act as a sedative in nervous disorders and induce sleep. An infusion of the bitter bark is taken as a tonic, stimulant, febrifuge and vermifuge.

The fresh young leaves contain as much as 300 mg of ascorbic acid per 100 g. The mature leaf contains 1-stachyhydrine.

Last updated: 4/2/99 by ch

Taste - A brief tutorial by Tim Jacol

Anatomy	Physiology	Transduction	Salt Taste	Sweet	Sour
Umami	Why Taste?	Taste Modification	Papillae	Cells	Receptors
Taste buds	Sweetners	Supertasters	Taste Maps	Strange facts	Bibliograpł

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Why taste?

Taste drives appetite and protects us from poisons. So, we like the taste of sugar because we have an absolute requirement for carbohydrates (sugars etc.). We get cravings for salt because we must have sodium chloride (common salt) in our diet. Bitter and sour cause aversive, avoidance reactions because most poisons are bitter (most bitter substances are bad for you - certainly in excess) and off food goes sour (acidic). Why do medicines all taste bitter? Because they are, in fact, poisons and if you take too much they will harm you. We have an absolute need for protein, and amino acids are the building blocks for proteins, so the "new" taste quality umami (pronounced: oo-marmi) which is the meaty, savoury taste drives our appetite for amino acids. This taste has been known to the Japanese for a long time - but has only recently been recognised by the West. Bacon really hits our umami receptors because it is a rich source of amino acids.

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Anatomy and Physiology of Gustation (taste)

In mammals taste buds are aggregations of 30-100 individual elongated "neuroepithelial" cells (50-60 microns in height, 30-70 microns in width), which are often embedded in specializations of surrounding epithelium, termed papillae. At the apex of the taste bud, microvillar processes protrude through a small opening, the taste pore, into the oral milieu. Just below the taste bud apex, taste cells are joined by tight junctional complexes.

Taste buds and taste papillae. Taste papillae can be seen on the tongue as little red dots, or raised bumps, particularly at the front of the tongue. These ones are actually called "fungiform" papillae, because they look like little button mushrooms. There are three other kinds of papillae, foliate, circumvallate and the non-gustatory filiform. Taste buds, on the other hand, are collections of cells on these papillae and cannot be seen by the naked eye. To illustrate the point, have a look at the diagram below. You can see that the taste buds are collections of cells situated on top of, or on the sides of, the different papillae.

h cf c b ff c b e ch g e e h

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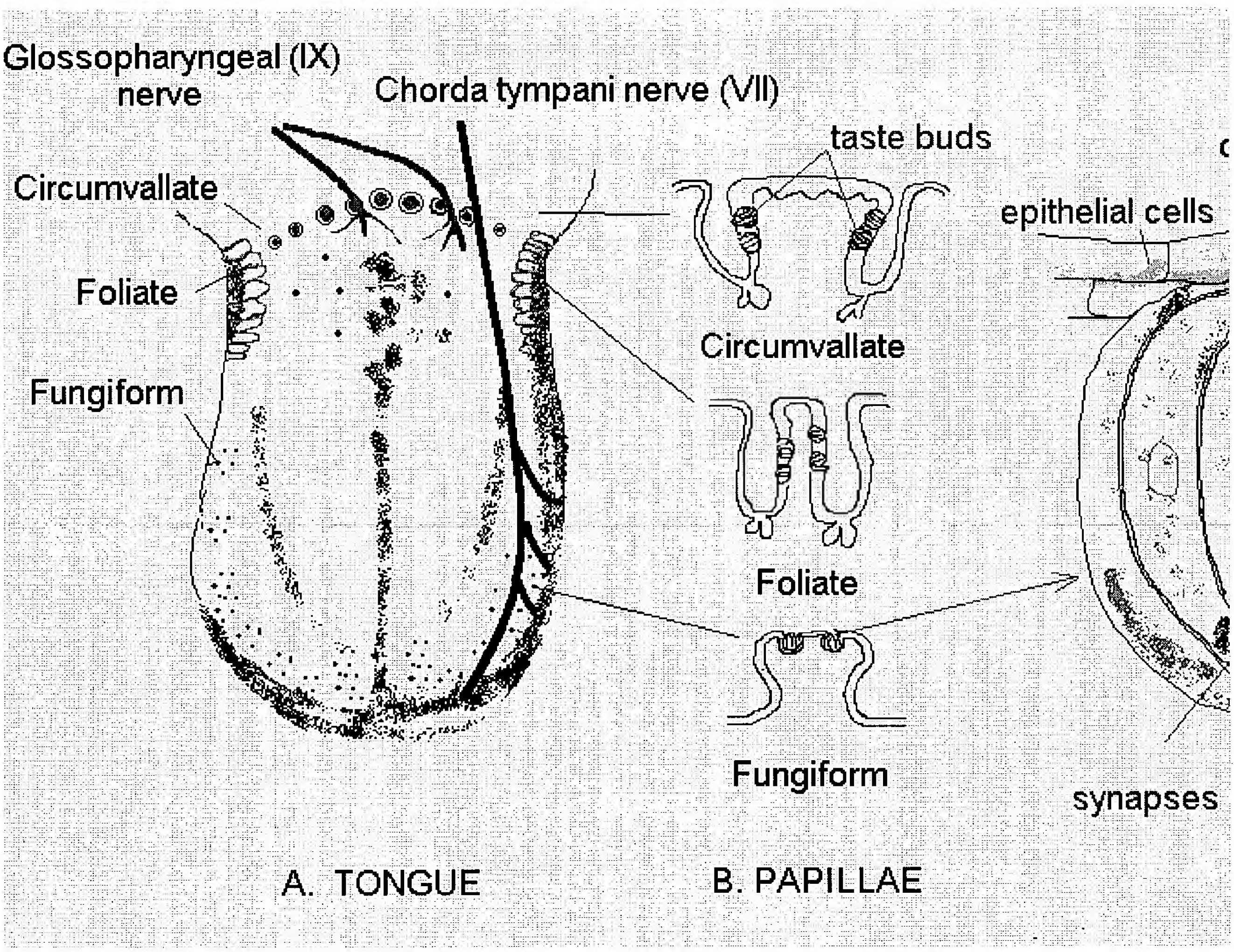
Figure 1.Papillae and taste buds



At the base of the taste bud, afferent taste nerve axons invade the bud and ramify extensively, each fibre typically synapsing with multiple receptor cells within the taste bud .Go to top

In mammals taste buds are located throughout the oral cavity, in the pharynx, the laryngeal epiglottis and at the entrance of the eosophagus. Taste buds on the dorsal lingual epithelium are the most numerous (total number of taste buds, all classes, = 4600 per tongue) and best-studied taste end-organs. Here, taste buds are contained within four major classes of papillae.

- *Fungiform papillae* are located on the most anterior part of the tongue and generally contain one to several taste buds per papilla. They are innervated by the chorda tympani branch of the facial (VIIth cranial) nerve. They appear as red spots on the tongue - red because they are richly supplied with blood vessels. The total number of fungiform papillae per human tongue is around 200. Papillae at the front of the tongue have more taste buds (1-18) compared to the mid-region (1-9). It has been calculated that there are 1120 fungiform taste buds per tongue.

- *Foliate papillae* are situated on the edge of the tongue slightly anterior of the circumvallate line. They are predominantly sensitive to sour tastes. Innervated by the glossopharyngeal (IXth cranial) nerve. On average 5.4 foliate papillae per side of the tongue, 117 taste buds per foliate papillae, total = 1280 foliate taste buds per tongue.
- *Circumvallate papillae* are sunken papillae, with a trough separating them from surrounding wall. The tase buds are in tiers within the trough of the papillae. They are situated on the circumvallate line and confer a sour/bitter sensitivity to the posterior 2/3 of the tongue. Innervated by the glossopharyngeal (IXth cranial) nerve. 3-13 circumvallate papillae per tongue with 252 taste buds per papillae, total = 2200 circumvallate taste buds per tongue
-  *Filiform papillae* (left) are mechanical and non-gustatory.

In addition there are 2500 taste buds on the epiglottis, soft palate, laryngeal and oral pharynx.

The number of taste buds declines with age.

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Cells in taste papillae

- *Supporting cells* - contain microvilli, appear to secrete substances into lumen of taste bud.
- *Sensory receptor cell* - has peg-like extensions projecting into lumen. These contain the sites of sensory transduction.
- *Basal cells* - these differentiate into new receptor cells. They are derived from surrounding epithelium. The cells are continuously renewed every 10 days or so.

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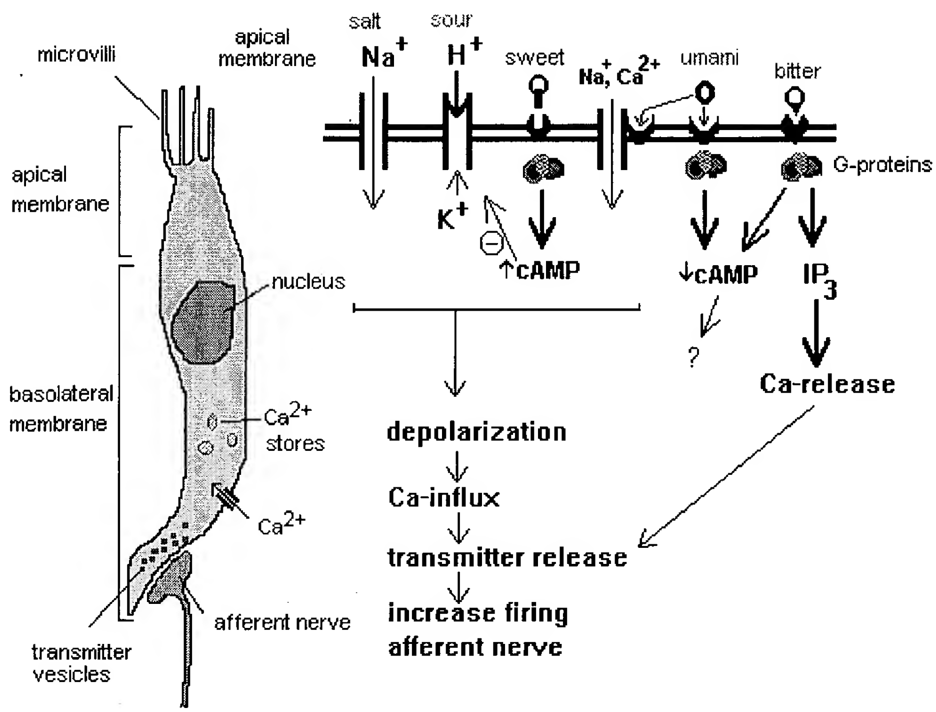
Figure 2. A taste receptor cell



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Taste transduction

There are five basic tastes: salt, sour, sweet, bitter and umami.

1. *Salt taste*
   Salt is sodium chloride (Na^+ Cl^-). Na^+ ions enter the receptor cells via Na-channels. These are amiloride-sensitive Na^+ channel (as distinguished from TTX-sensitive Na^+ channels of nerve and muscle). The entry of Na^+ causes a depolarization, Ca^{2+} enters through voltage-sensitive Ca^{2+} channels, transmitter release occurs and results in increased firing in the primary afferent nerve.
2. *Sour taste*
   Sour taste is acid and acid is protons (H^+). H^+ ions block K^+ channels. K^+ channels are responsible for maintaining the cell membrane potential at a hyperpolarized level (close to the K^+ equilibrium potential of around -85mV). Block of these channels causes a depolarization, Ca^{2+} entry, transmitter release and increased firing in the primary afferent nerve. Go to top
3. *Sweet taste*
   There are receptors in the apical membrane that bind glucose (sucrose - a combination of glucose and fructose - and other carbohydrates). Binding to the receptor activates adenylyl cyclase, thereby elevating cAMP. This causes a PKA-mediated phosphorylation of K^+ channels, inhibiting them. Depolarization occurs, Ca^{2+} enters the cell through depolarization-activated Ca^{2+} channels, transmitter is released increasing firing in the primary afferent nerve.
4. *Bitter taste*

Bitter substances cause the second messenger (IP_3) mediated release of Ca^{2+} from internal stores (external Ca^{2+} is not required). The elevated Ca^{2+} causes transmitter release and this increases the firing of the primary afferent nerve.

5. *Umami taste*
   Umami is the taste of certain amino acids (e.g. glutamate, aspartate and related compounds). It was first identified by Kikunae Ikeda at the Imperial University of Tokyo in 1909. Recently it has been shown[1,2] that the *metabotropic* glutamate receptor (mGluR4) mediates umami taste. Binding to the receptor activates a G-protein and this may elevate intracellular Ca^{2+}. (Go to top)
   Monosodium glutamate, added to many foods to enhance their taste (and the main ingredient of Soy sauce), may stimulate the umami receptors. But, in addition, there are *ionotropic* glutamate receptors (linked to ion channels), i.e. the NMDA-receptor, on the tongue. When activated by these umami compounds or soy sauce, non-selective cation channels open, thereby depolarizing the cell. Calcium enters, causing transmitter release and increased firing in the primary afferent nerve

   [1]Chaudhari et al, (1996) The taste of monosodium glutamate: membrane receptors in taste buds. J. Neurosci. 16, 3817-3826.
   [2]Kurihara & Kashiwayanagi (1998) Introductory remarks on umami taste. Annals NY Acad Sci 855, 393-397.

6. *Monosodium glutamate*
   Monosodium glutamate is the main ingredient of Soy sauce. This is added to foods to enhance their flavour. It probably works by activating NMDA receptors which are found in taste cells. NMDA receptors are integral receptor-ion channel complexes and when they open they allow an influx of Na^+ and Ca^{2+} ions. This will depolarise the taste receptor cell and act as an excitatory influence. Then, far less of a particular taste will be required to cause the further depolarisation necessary to bring about transmitter release.

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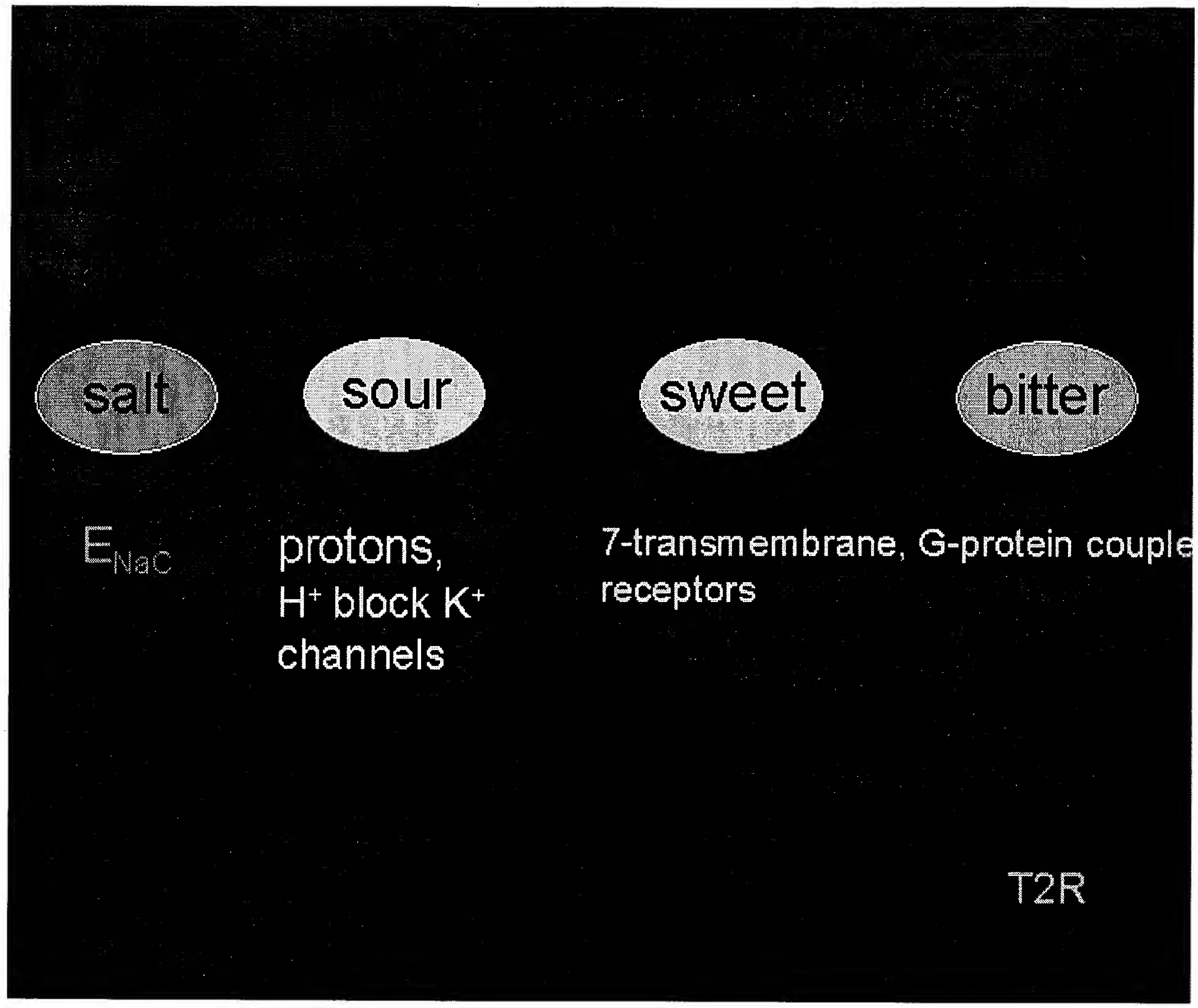
Receptors

Sweet and bitter taste receptors have recently been cloned. A summary of the different types of receptor responsible for each of the 5 taste modalities is given below.



Salt receptor

- ENaC (Epithelial Sodium (Na) channel)
- ubiquitously expressed
- only functional in anterior tongue

Bitter receptor family - T2Rs

- 50-80 members
- expressed in small subset of all taste papillae
- expressed in cells that also express a-gustducin
- 70% of gustducin cells in circumvallate & foliate papillae express T2Rs

Sweet and umami receptors
Heteromeric receptors made up of a combination of different subunits, coded for by a small gene family - T1R

h cf c b ff c b e ch g e e h

- T1Rs (3 genes distantly related to mGluRs)
- T1R1 - expressed in fungiform papillae
- T1R2 - expressed in circumvallate & foliate
  - both may couple with transducin, not gustducin
- T1R3 - expressed in 30% of all taste buds
- T1R1+3 = amino acid receptor (umami)
- T1R2+3 = sweet receptor
- Umami is possibly mediated by both mGluR4 and T1R1+3 receptors

Sour receptors

Sour is the taste of acid, i.e. protons (H^+). Three possible receptor mechanisms:

- H^+ blocks K^+ channels
- H^+ ions go through ENaC channels
- H^+ ions go through a proton channel

References for taste receptors
(1) Mammalian Sweet taste receptors. Nelson, G. et al (2001) Cell, 106, 381-390
(2) An amino-acid taste receptor. Nelson, G. et al (2002) Nature 416 (14 March), 199-204
(3) A plethora of taste receptors. Kinnamon, S.C. (2000) Neuron, 25, 507-510.

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Artificial Sweetners

Saccharin - Discovered in 1879 when a Johns Hopkins worker inadverently licked his fingers. Saccharin is only sweet to humans. Bees/butterflies which normally crave the sweetness of nectar, do not treat it as a desirable substance.

Cyclamate - Discovered by accident. A graduate student at the University of Illinois in 1937 was smoking a cigarette that came into contact with some.

Aspartame - James Schlatter licked fingers in preparing to pick up a peice of weighing paper. It is a combination of two naturally occurring amino acids (aspartic and phenylalanine). Alitame, similar to aspartame in that it combines two amino acids (alanin and aspartic acid) into a dipeptide, is about 2,000-times sweeter than sugar.

Have a look at the structure of sweetners

Sucralose - A chloride-containing carbohydrate product some 600-times sweeter than sugar. Discovered when a foreign student (Shashikant Phadnis) working in Prof Leslie Hough's lab at King's College, London, misunderstood a request for "testing" as "tasting".

Some plant proteins, e.g. Monellin and Thaumatin, taste 10,000 times as sweet as sucrose (a disaccharide made up of a glucose and a fructose molecule). Salts of lead and beryllium also taste sweet.

Certain artifical sweetners (e.g. saccharin) lead to the generation of IP_3 and a rise in intracellular Ca^{2+} due to release from internal stores.

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Modifying taste

Taste exhibits almost complete adaptation to a stimulus - perception of a substance fades to almost nothing in seconds. Taste can be suppressed by local anaesthetics applied to the tongue. Amiloride, a blocker of epithelial Na channels, reduces salt taste in humans and adenosine monophosphate (AMP) may block the bitterness of several bitter tasting agents. Naturally occuring compounds include, gymnemic acid (a product of the Indian tree/shrub Gymnema sylvestre) decreases the sweet perception by competitive inhibition of the sweet receptor. Artichokes have the opposite effect, enhancing sweet taste (the active compounds in this case are chlorogenic acid and cynarin) by suppression of sour and bitter taste receptors. Miracle fruit turns sour tastes sweet. The active ingredient, "miraculin", binds to a site near the sweet receptor. When sour substances then are tasted, a conformational change in the taste cell membrane occurs in such a way as to bring the miraculin molecule into contact with the sweet receptor, activating it.

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Regional localisation of taste on the tongue (Taste maps)

There has been some controversy as to whether the familiar taste maps of the human tongue, which appear in every textbook, are correct. Taste sensation can be localised on the tongue but does the tongue have regions that are more sensitive to one taste modality than another? Fungiform papillae are concentrated on the anterior tip of the tongue and anterior lateral margins in humans and it has been demonstrated that NaCl threshold was inversely related to the number of fungiform papillae (more papillae = more sensitivity, lower threshold). In a study of human fungiform papillae it was found that taste buds can respond to NaCl only or to both NaCl and sucrose. The responses to NaCl and sucrose occurred in different cells within the taste bud. Thus, one can infer that fungiform papillae are salt-sensitive but this does not mean they are insensitive to other tastes. Bitter receptors are not uniformly distributed over the tongue. In rats the bitter receptors are expressed in a subset of taste cells in all papillae but they are more concentrated in foliate and circumvallate papillae situated at the sides and the back of the tongue. Furthermore, alpha-gustducin, which is the G-protein coupled to the T2R bitter receptors (see below), is expressed more in circumvallate than fungiform papillae in the rat. One rather more empirical approach to resolving this question is to stimulate the different areas of the tongue directly. Thermal stimulation of the anterior sides of the tongue in humans (fungiform papillae and the chorda tympani nerve) evokes sweet and salt/sour taste. While thermal stimulation of the rear of the tongue (foliate/circumvallate papillae and glossopharyngeal nerve) causes a different relationship between temperature and taste to the anterior stimulation. One can conclude that the classical "taste map" is an over simplification. Sensitivity to all tastes is distributed across the whole tongue and indeed to other regions of the mouth where there are taste buds (epiglottis, soft palate), but some areas are indeed more responsive to certain tastes than others.

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Relay to the brain

Figure 3. Innervation of the tongue

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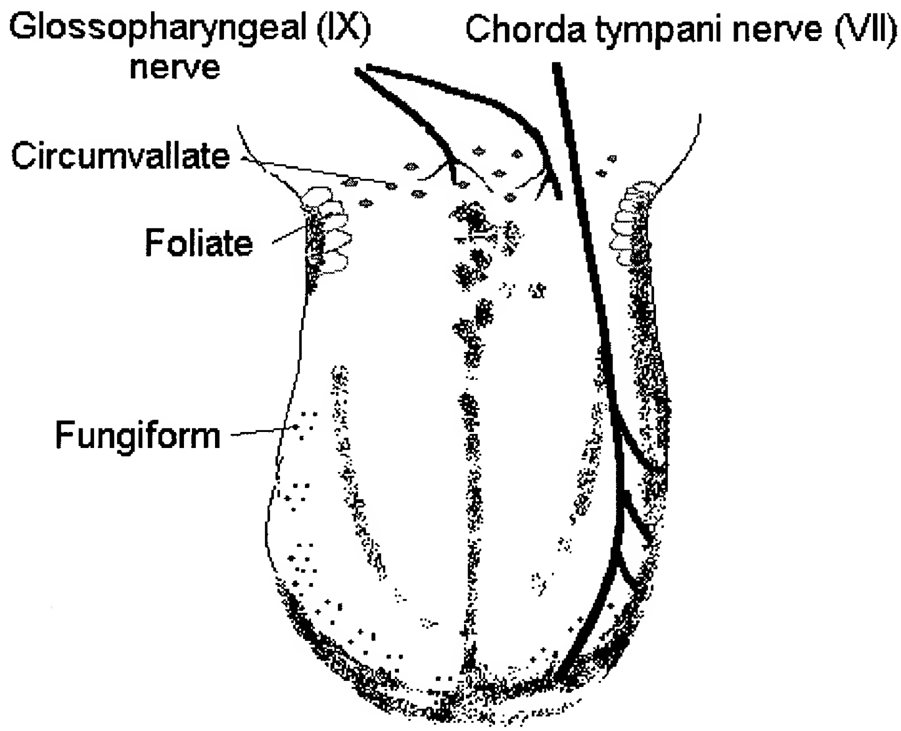

Taste receptor cells do not have an axon. Information is relayed onto terminals of sensory fibres by transmitter. These fibres arise from the ganglion cells of the cranial nerves VII (facial - a branch called the chorda tympani)) and IX (glossopharyngeal) (see Figure 2).The first recordings from sensory fibres showed an optimal response to one stimuli, but a smaller response to other taste stimuli.

Taste is determined by the pattern of active (firing) fibres, i.e. by "across-fibre pattern" rather than "labelled-line".

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Central pathways
Primary gustatory fibres synapse centrally in the medulla (in a thin line of cells called the nucleus of the solitary tract). From there the information is relayed (1) to the somatosensory cortex for the conscious perception of taste and (2) to the hypothalamus, amygdala and insula, giving the so-called "affective" component of taste. This is responsible for the behavioural response, e.g. aversion, gastric secretion, feeding behaviour.

Supertasters

It has been found that some people have more than the normal number of taste papillae (and taste buds). They are distinguished by their increased density of fungiform papillae and their exterme sensitivity to the chemical *n*-propylthiouracil (PROP). Supertasters - 25% of the population (and more women than men) - tend not to like green vegetables and fatty foods.

	% of population	*density of taste papillae cm^{-2}
supertasters	25	165

h cf c b ff c b e ch g e e h

normal tasters	50	127
non-tasters	25	117

* at the tip of the tongue (from Yackinous & Guinard, *Appetite* (2000) **38**, 201-209).

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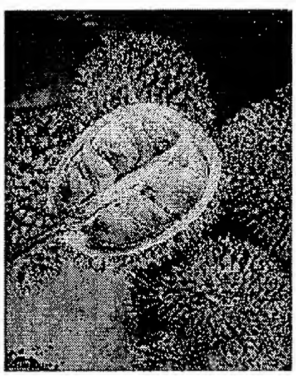
Strange taste facts

Taste is mainly smell. Hold your nose, close your eyes, and try to tell the difference between **coffee** or **tea**, **red** or **white** wine, **brandy** or **whisky**. In fact, with blocked nose (clothes peg or similar) you can't tell the difference between grated apple and grated onion - try it! Of course, this is because what we often call taste is in fact flavour. Flavour is a combination of taste, smell, texture (touch sensation) and other physical features (eg. temperature).



Smelly fruit

The durian fruit smells horrible. Some people cannot bear to eat it because it smells so foul. But it is called the "King of Fruits" and tastes delicious. It is very large (can be the size of a football) and comes from South East Asia.

Links to other sites:

- Notes on smell
- Chemoreception, a vaste resource of everything to do with taste and smell, wierd and mainstream.

Return to Teaching Menu or Tim Jacob homepage

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- Handbook of olfaction and gustation by Doty, R.L. (1995). Marcel Dekker.

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